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Inter-subspecific Hybridizations in *Senecio glaucophyllus* Cheesem.

By ROBERT ORNDUFF

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Summary

RESULTS of hybridizations among and within the subspecies of *Senecio glaucophyllus* Cheesem. are reported. The average pollen fertility of F_1 progenies is generally high, although a decrease in pollen fertility may occur in the F_2 generation. It is suggested that some of the variation in this polymorphic species may be attributed to hybridization between the subspecies which followed European settlement of New Zealand.

INTRODUCTION

Senecio glaucophyllus Cheesem. (Compositae: Senecioneae) is a member of the *Senecio lautus* complex in New Zealand, which also includes *S. lautus* Willd., $n = 20$; *S. sterquilinus* Ornduff, $n = 20$; *S. radiolatus* F. Muell., $n = 40$; and *S. antipodus* Kirk, n unknown. A recent taxonomic revision of these New Zealand members of the group (Ornduff, 1960) differed from traditional treatments in transferring some infraspecific taxa formerly referred to *S. lautus* from that species to *S. glaucophyllus* and in suggesting that the New Zealand plants of *S. lautus* should be considered taxonomically distinct from plants in Australia also called by that name.

Results of morphological studies were the primary bases for the taxonomic treatment of the species complex, but much useful information came from a variety of other sources, including a hybridization programme which was discussed only briefly. The purpose of this paper is to report the results of the crossing programme within *S. glaucophyllus* and to discuss briefly the relevance of these results to recent evolutionary patterns in the species.

GENERAL CONSIDERATIONS

Senecio glaucophyllus is a perennial herb which occupies a wide range of habitats in the North and South Islands of New Zealand. The four subspecies recognized (Ornduff, 1960) are distinguished primarily on their morphology, but

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largely occupy distinct habitats and geographical areas. Chromosome numbers of n = 50 have been determined for three of the subspecies; this number is unknown in other Senecios (Cave, 1958–1960; Darlington and Wylie, 1956). Morphological variation within the subspecies is considerable and some populations are known which possess plants combining characters of two or more subspecies. Major emphasis was placed on hybridizations in various combinations among the subspecies in the hope of determining the genetic affinities between plants differing widely in morphology and habitat. In addition, it was hoped that studies on the F_1 hybrids and their segregates would shed light on the nature and origin of some of the intermediate populations known to occur in the field.

The subspecies of *S. glaucophyllus* have been described and illustrated elsewhere (Ornduff, 1960) and will be only briefly characterized here. They are:

1. *Senecio glaucophyllus* subsp. *glaucophyllus*: An erect, long-lived perennial to 60 cm tall, branched from the base; middle cauline leaves sinuate-dentate to serrate; heads borne in a corymb; ray florets present. Apparently largely confined to limestone crevices in Tasman and Lyell Ranges, and possibly the Richmond Range; alt. 2,000–4,000ft.

2. *S. glaucophyllus* subsp. *basinudus* Ornduff: An erect to prostrate, short-lived perennial; similar to above subsp. but differing in lacking basally-clustered shoots to which the plants die back in winter; heads borne loosely, not in a corymbose arrangement. Dunes and cliffs along the sea-coast, eastern coast of the South Island.

3. *S. glaucophyllus* subsp. *raoulii* (Hook. f.) Ornduff: An erect, long-lived perennial herb to 60 cm tall, branched from the base; middle cauline leaves deeply pinnatifid; heads borne in dense corymbiform panicle; ray florets present. Rocky cliffs, amongst tussock, or on shingle, North Island volcanic plateau, Marlborough, and northern Canterbury; alt. 1,500–4,800ft.

4. *S. glaucophyllus* subsp. *discoideus* (Cheesem.) Ornduff: An erect to lax-stemmed, long-lived perennial to 25 cm tall; middle cauline leaves serrate to deeply pinnatifid; heads single or few, discoid. Unstable shingle slips east of main divide of South Island mountains and rarely North Island; alt. 2,000–5,000ft.

HYBRIDIZATIONS

Plants from various localities in New Zealand were grown in the greenhouse at the University of Washington, Seattle (see Table I). Cultivation was easy and flowering occurred as early as 14 weeks after sowing. Most of the distinctive features of the subspecies were retained in cultivation, although some differences in stature, size of plant, succulence, and degree of leaf dissection were noted in these plants when compared with their field-collected parents. All subspecies appear to be self-compatible, but largely outbreeding, although *Senecio glaucophyllus* subsp. *discoideus* sets a high amount of selfed fruits even if visited freely by pollinators. Occasional plants of some subspecies were pollen-sterile but produced copious fruits when pollinated by other plants. These pollen-sterile plants were generally avoided in the crossing programme, although the only plants available of *S. glaucophyllus* supsp. *glaucophyllus* were pollen-sterile. The genetics of this trait is unknown, but both pollen-producing and pollen-sterile plants may occur as siblings in the same progeny.

Immature flower heads were emasculated by removing their upper portion with a razor blade and repeatedly washing the cut surface to remove any remaining pollen. These heads were bagged and pollen from the desired parent applied until the recipient styles withered, indicating pollen-tube growth. Both crossability among the subspecies and germinability of the fruits are very high. The fruits require no dormant period and were sown immediately after harvesting; from 4 to 12 plants in each progeny were grown. Pollen was collected from these plants, mounted in aniline blue—lactophenol, and the per cent fertility determined by counting the stained grains in a sample of 200.

TABLE I.

	Subspecies	Abbreviation	Locality	Collector	Average Pollen Fertility male sterile
1.	*glaucophyllus*	ART	Mt Arthur, Nelson (topotype)	G. G. Pritchard	
2.	*basinudus*	AB	Allans Beach, near Dunedin	G. T. S. Baylis	100%
		PH	Lake Ellesmere, near Christchurch (isotypes)	J. W. Dawson	97%
3.	*raoulii*	RUA	Moemoe, N.W. Ruahines	R. Ornduff *et al.*	95%
		NGAR	Near confluence of Ngaruroro and Te Matia rivers, North Island	N. L. Elder	95%
		POHA	Pohatuhaha, Ruahine Range	N. L. Elder	90%
4.	*discoideus*	BC	Bluecliffs Station, west of St. Andrews	Mrs P. Woodhouse	100%
5.	intermediate *discoideus-raoulii*	MOLE	Big Hill, Molesworth	M. Simpson	95%

Results of the hybridizations are summarized in Table II. For each entry, the taxonomic status of the plants is given, followed by the abbreviation of their place of origin listed in Table I. The maternal parent is listed first. The per cent figure given after the colon is the average pollen fertility of the progeny of that cross; if a second per cent figure is given (after a semi-colon), it is the average fertility of the hybrid progeny of the reciprocal cross. Numbers in parentheses after some hybrid fertilities indicate the range of pollen fertility within a progeny if it exceeded 10 per cent.

TABLE II.

A. Crosses within the subspecies:
   1. *glaucophyllus*: none
   2. *discoideus*: none
   3. *basinudus*: AB x PH: 94% (83–100); 97%
   4. *raoulii*: NGAR x MOLE: 80%
      POHA x MOLE: 99%

B. Crosses between subspecies:
   1. *glaucophyllus* x *basinudus*: ART x AB: 89%
   2. *basinudus* x *raoulii*: PH x RUA: 91%; 93% (83–98)
      AB x RUA: 91% (85–97)
   3. *basinudus* x *discoideus*: PH x BC: 94%
   4. *discoideus* x *raoulii*: BC x RUA: 87% (82–93)
      BC x POHA: 98%; 98%

C. F_2 generations:
   1. *basinudus* x *discoideus* (PH x BC): 86% (70–98)
   2. *discoideus* x *raoulii* (BC x RUA): 61% (21–76)

DISCUSSION

Nearly every possible hybrid combination among the subspecies of *S. glaucophyllus* was made, but only a few could be grown because of restricted greenhouse space. Nevertheless, certain generalizations may be made. The pollen fertilities of all F_1 progenies are high, although frequently they are lower than pollen fertility of parents. The lowest average F_1 fertility recorded (80%) is only 10% lower than that of one natural population (POHA: 90%) and should be considered relatively high, especially when it is compared with the total absence of stainable pollen produced by some interspecific hybrids in the *Senecio lautus* complex (Ornduff, 1956). There is no apparent difference between fertility of intra-subspecific hybrids and that of inter-subspecific hybrids, nor is there any

positive correspondence between place of parental origin—either geographically or ecologically—and fertility of hybrids. Crosses between plants from the North and South Islands, or from high mountains and the sea-coast produce no less fertile offspring than crosses between plants originating in similar or nearby localities.

The range of fertility within the two F_2 progenies grown exceeded that in the F_1 progenies. The average fertility of the F_2 progeny derived from PH x BC was a little lower than that of the F_1, although the most fertile individuals in this F_2 were as fertile as those in the F_1. In contrast, a considerably reduced average fertility was recorded for the F_2 derived from BC x RUA, and the most fertile individuals in this F_2 were less fertile than the least fertile plant of the F_1. Neither of these F_2 generations was obtained in lines in which pollen-sterility had been observed.

It is evident that despite the wide range of variation both in morphology and habitat occupied by the races of *Senecio glaucophyllus*, even plants most divergent in these respects have retained sufficient genetic identity to exchange genes, at least in the greenhouse. There is no evidence of cytological aberrations in the hybrids, suggesting that intraspecific differentiation has been primarily at a genic, rather than a cytological level, although cryptic structural repatterning of the chromosomes may have occurred (Stebbins, 1950) which does not greatly affect fertility of the hybrids. This is in keeping with the idea that primary evolutionary emphasis is placed on adaptation of plants to their environment, and that sterility barriers, at least between largely allopatric taxa, are built up only incidentally. It is possible, of course, for potentially infertile taxa to retain their distinctiveness because of effective natural barriers to gene exchange such as phenological differences, selective pollinators, or geographical isolation.

For the most part, the subspecies of *Senecio glaucophyllus* are allopatric, although some overlap in range does occur. In these areas, some individuals are not readily referable to the recognized subspecies, but combine the features of two or more of them. For example, on the seaward side of the northern portion of the range of *S. glaucophyllus* subsp. *discoideus* plants have been collected which show intermediacy between this subspecies and subsp. *raoulii*. A sample from one of these populations (MOLE) was grown in the greenhouse and did not show segregation for its intermediate characteristics in the F_2 or subsequent generations, whereas segregation for some features in the artificial F_2 progenies mentioned above was noted. These observations suggest that at least some of the naturally-occurring intermediate populations are not of immediate hybrid origin, although their combination of characteristics is likely due to hydridization within relatively recent times.

It is probable that the ecologically and morphologically distinctive races of *Senecio glaucophyllus* developed in New Zealand long before European colonization. Subsequent severe disturbances of the native vegetation occurred following European settlement (Oliver, 1955; Thomson, 1922) which resulted in the breakdown of natural barriers to intercrossing of these races in some areas. *Senecio glaucophyllus* occurs largely in unforested regions, the extent of which has been considerably increased in the last century either directly or indirectly by man (Cockayne, 1928).

Natural hybridization is frequently associated with such disturbances (Anderson, 1948; Stebbins, 1959). A large number of new genotypes results from such hybridization, and it is from these and their segregates that new races may be selected which are adapted to the new conditions in the field. Much more work on *S. glaucophyllus* remains to be done, but the results of the artificial hybridizations are not incompatible with the speculation that the populations showing

some degree of intermediacy between the subspecies may ultimately be traced to natural hybridization.

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ROBERT ORNDUFF, B.A., M.Sc., Ph.D.
Department of Botany,
Duke University,
Durham, North Carolina.